NeoBiota 44: 75–93 (2019)
doi: 10.3897/neobiota.44.33771
http://neobiota.pensoft.net

DATA PAPER

A peer-reviewed open-access journal
NeoBiota
Advancing research on alien species and biological invasions

The dark side of facilitation: native shrubs facilitate exotic annuals more strongly than native annuals

Jacob E. Lucero[1,2], Taylor Noble[3], Stephanie Haas[1], Michael Westphal[4], H. Scott Butterfield[5], Christopher J. Lortie[1]

1 *Department of Biology, York University, Toronto, Ontario M3J1P3, Canada* **2** *Division of Biological Sciences and Institute on Ecosystems, University of Montana, Missoula, MT 59812, USA* **3** *US Fish and Wildlife, U.S. Fish and Wildlife Service, Northern Indiana, P.O. Box 2016 Chesterton, Indiana 46304, USA* **4** *Bureau of Land Management, Central Coast Field Office, 940 2nd Avenue, Marina, CA 93933, USA* **5** *The Nature Conservancy, 201 Mission Street, 4th Floor, San Francisco, CA 94105, USA*

Corresponding author: *Jacob E. Lucero* (jelucero@yorku.ca)

Academic editor: *M. Rejmanek* | Received 9 February 2019 | Accepted 19 March 2019 | Published 5 April 2019

Citation: Lucero JE, Noble T, Haas S, Westphal M, Butterfield HS, Lortie CJ (2019) The dark side of facilitation: native shrubs facilitate exotic annuals more strongly than native annuals. NeoBiota 44: 75–93. https://doi.org/10.3897/neobiota.44.33771

Abstract

Positive interactions enhance biodiversity and ecosystem function, but can also exacerbate biological invasions. Facilitation of exotic invaders by exotic foundation species (invasional meltdown) has been studied extensively, but facilitation of exotic invaders by native foundation species has attracted less attention. Specifically, very few studies have examined the extent that native foundation species facilitate native and exotic competitors. Understanding the processes that mediate interactions between native and exotic species can help explain, predict, and improve management of biological invasions. Here, we examined the effects of native foundation shrubs on the relative abundance of the annual plant community – including native and exotic taxa – from 2015–2018 in a desert ecosystem at Carrizo Plain National Monument, California, USA (elevation: 723 m). Shrub effects varied by year and by the identity of annual species, but shrubs consistently enhanced the abundance of the annual plant community and facilitated both native (n=17 species) and exotic (n=4 species) taxa. However, at the provenance level, exotic annuals were facilitated 2.75 times stronger in abundance than native annuals, and exotic annuals were always more abundant than natives both near and away from shrubs. Our study reaffirms facilitation as an important process in the organisation of plant communities and confirms that both native and exotic species can form positive associations with native foundation species. However, facilitation by native foundation species can exacerbate biological invasions by increasing the local abundance of exotic invaders. Thus, the force of facilitation can have a dark side relevant to ecosystem function and management.

Copyright *Jacob E. Lucero et al.* This is an open access article distributed under the terms of the Creative Commons Attribution License (CC BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Keywords
Bromus rubens, deserts, exotic species, facilitation, invasional meltdown, native species, plant invasions, shrubs

Introduction

Positive interactions among species, or facilitation, can strongly influence the organisation of plant communities (Callaway 1995; Callaway 2007; Brooker et al. 2008), particularly in unproductive environments (Bertness and Callaway 1994; Maestre et al. 2009). Facilitation occurs when a foundation species ameliorates biotic or abiotic stresses that would otherwise inhibit the abundance, richness, fitness, and/or population growth of beneficiary species (Callaway 2007). For example, foundation shrubs in deserts can provide annual species with refuge from solar radiation and/or drought, resulting in increased richness and abundance of annual species inside shrub canopies relative to outside of canopies (Filazzola and Lortie 2014). Importantly, beneficiary species can experience facilitation from foundation species and interspecific competition from other beneficiary species simultaneously, which can influence the net outcome of biotic interactions (Poulos et al. 2014; Sheley and James 2014; Wright et al. 2014). Regardless, facilitation generally enhances biodiversity (Butterfield et al. 2013; McIntire and Fajardo 2014) and ecosystem function (Michalet 2006; Callaway 2007; Michalet and Pugnaire 2016).

However, facilitation can have a dark side when beneficiary species are exotic invaders. Invasive plant species pose a pervasive threat to ecosystem function worldwide (Simberloff et al. 2013), including strong effects on historic patterns of nutrient cycling (Liao et al. 2008), energy flow (Baxter et al. 2004; Pearson and Callaway 2008), and abiotic disturbance (D'Antonio and Vitousek 1992; Balch et al. 2013). These disruptions are often associated with sharp reductions in local biodiversity (Vila et al. 2011; Bellard et al. 2016). Interestingly, positive interactions have been shown to promote the success of invasive species in non-native communities (Simberloff 2006; Griffith 2010). Exotic invaders are commonly facilitated by exotic species (reviewed by Simberloff 2006), and such "invasional meltdown" (Simberloff and Von Holle 1999) is a leading hypothesis in invasion biology (Jeschke et al. 2012). Native foundation species can also facilitate exotic invaders, especially in harsh environments (Lenz and Facelli 2003; Cavieres et al. 2008; Altieri et al. 2010; Griffith 2010; Zarnetske et al. 2013; Badano et al. 2015; Hupp et al. 2017). However, native-invader facilitation has attracted less attention than the invasional meltdown hypothesis. Furthermore, very few studies have specifically addressed whether native foundation species in drylands benefit native and exotic beneficiary species to the same extent (but see Reisner et al. 2015; Ramírez et al. 2015). The biogeographic origins (i.e., provenance) of beneficiary species is an important consideration because exotic species displace native species in drylands globally (Balch et al. 2013; Bellard et al. 2016; Vitousek et al. 2017), and facilitation by native foundation species can influence the outcome of interactions between native and exotic taxa (Reisner et al. 2015). Strong facilitation of exotic species relative to native competitors could require conservationists to shift their focus from

manipulating competitive interactions to facilitative ones in order to manage biological invasions (Funk et al. 2008).

The objective of this study was to investigate the extent that native and exotic species of annual plants associate with (i.e., are facilitated by) native foundation shrubs in an arid ecosystem. This issue is timely because drylands worldwide are increasingly comprised of exotic species (Vitousek et al. 2017; Simpson and Eyler 2018), and facilitation by native foundation species has considerable potential to be used as a tool for restoring native biodiversity to drylands degraded by biological invasions and other anthropogenic disturbances (Padilla and Pugnaire 2006; Funk et al. 2008; Gomez-Aparicio 2009; Lortie et al. 2018c). Specifically, we examined the hypothesis that native and exotic annual species can associate differentially with native foundation shrubs. We tested the following predictions: (i) the net abundance of the annual plant community is greater near native foundation shrubs than away from shrubs; (ii) native and exotic annual species can both associate with native foundation shrubs to become beneficiary species; and (iii) the strength of facilitation depends upon the provenance of beneficiary species. To better understand community-level outcomes of biotic interactions, we also evaluated correlations between the abundance of native and exotic annual species near and away from native foundation shrubs.

Methods

Study site and species

We surveyed annual plant communities at Carrizo Plain National Monument in the San Joaquin Desert (Germano et al. 2011) of California (35.1N, 119.6W, elevation: 723 m) at peak flowering from March to April from 2015 to 2018 at a total of seven study sites (Suppl. material 1: Table A1). This area is characterised as an arid grassland (Buck-Diaz and Evens 2011), but the native shrubs *Ephedra californica*, *Gutierrezia californica*, and *Atriplex polycarpa* are also present (U.S. Department of the Interior 2011). Here, we explored the potential for *E. californica*, the most abundant shrub species at our sites (Buck-Diaz and Evens 2011; Noble et al. 2016), to act as a foundation species. *Ephedra californica* is a long-lived perennial associated with the creosote scrublands, chaparral, and arid grasslands of southwestern North America (Cutlar 1939) and can facilitate native annuals (Lortie et al. 2018a) and endangered vertebrates (Filazzola et al. 2017; Westphal et al. 2018). We sampled a total of 21 annual plant species throughout the study (Suppl. material 1: Table A2), including 17 native and 4 exotic species. Among the exotic species sampled was *Bromus madritensis* ssp. *rubens* (*B. rubens* hereafter), one of the most problematic exotic invaders in the region (Salo 2005). Annual precipitation, mean annual temperature, and mean winter temperature at the study sites ranged from 116.22–129.44 mm, 17.5–18.0 °C, and 10.19–12.14 °C, respectively (Suppl. material 1: Table A2).

Sampling

We sampled the abundance of the annual plant community using a paired shrub-open microsite contrast with 0.5 × 0.5 m quadrats (Pescador et al. 2014). Shrub microsites were defined as the area immediately beneath the canopy of *E. californica* shrubs, and open microsites were defined as interstitial spaces at least 1 m from any shrub canopy. We did not sample areas more than 5 m away from shrubs. A total of 1194 independent pairs of shrub and open microsites were sampled, and repeated-measures were avoided by randomly selecting sampling locations at each site for each year. The size of foundation plants can influence the direction and magnitude of their effects on neighbours (Tewksbury and Lloyd 2001; Miriti 2006; Brathen and Lortie 2015). To account for this, the height, width, and perpendicular width (m) of each foundation shrub were measured, and the volume for a sphere was used to summarise shrub sizes (m^3) as a covariate in subsequent analyses. Across all study sites, mean shrub width was 2.80 m ± 0.03 SE, mean shrub volume was 23.65 m^3 ± 0.26 SE, and mean shrub density was 44.43 shrubs/ha ± 8.98 SE. These measurements are well within ranges reported by other studies in similar systems (e.g., Lortie et al. 2018a). We recorded the total abundance of each annual species present in sampling quadrats, and the provenance of each annual species was retrieved from the CalFlora database (CalFlora 2018). Individuals were easy to distinguish because the annual species we sampled do not reproduce asexually. Data are publicly archived (Lortie et al. 2018b).

Statistical analyses

Relative interaction indices ("RIIs" hereafter; Armas et al. 2004) were used to estimate the effects of *E. californica* shrubs on the relative abundance of annual species. We calculated RIIs as follows:

$$RII = \frac{A_s - A_c}{A_s + A_c}$$

where A_s is the abundance (i.e., no. individual plants) of an annual species in a shrub microsite and A_c is the abundance of the same annual species in the paired open microsite. RII values range from -1 to +1. Negative RII values indicate negative (competitive) effects of shrubs on annual species, positive values indicate positive (facilitative) effects, and a value of 0 indicates a neutral effect. Annuals are only considered to be beneficiary species of foundation shrubs when RII is positive.

To evaluate whether annual species were generally more abundant near *E. californica* shrubs than away from shrubs, we performed independent one-sample *t*-tests with mean RII (pooled per species per year) as the response variable for each year of the study. We used an additional one-sample *t*-test to summarise the net strength of shrub associations across all study years. We evaluated the net strength of species-specific shrub associations using a linear mixed-effects model with RII (pooled per species per year) as the response variable, species identity and shrub volume as fixed factors, and

study year as a random factor. Treating year as a random factor accounted for stochastic sources of inter-annual variation, such as climate (Suppl. material 1: Table A2).

To test whether native and exotic annual species associated differentially with *E. californica* at the provenance level, we employed independent generalised linear models for each year of the study with RII (pooled per species) as the response variable and species provenance as a fixed factor. We contrasted the net strength of native vs. exotic associations with shrubs across all study years using a linear mixed-effects model with RII (pooled per species per year) as the response variable, species provenance and shrub volume as fixed factors, and study year as a random factor.

We inferred the outcome of biotic interactions between native and exotic annuals at the provenance level using *t*-tests and linear models. For shrub and open microsites and for each year of the study, we contrasted the net abundance of native vs. exotic annuals using independent one-sample *t*-tests with abundance (i.e., not RIIs) as the response variable. We then regressed net native abundance against net exotic abundance using linear models. These regressions addressed the effects of exotic annual species on the abundance of native annual species. Negative line slopes suggested competitive effects; positive line slopes suggested facilitative effects (Pearson et al. 2016).

All analyses were performed in R, version 3.5.1 (R Development Core Team 2018). All linear mixed-effects models used the lmer function of the lmerTest package (Kuznetsova et al. 2018). *T*-tests, generalised linear models, and linear models used the t.test, glm, and lm functions, respectively (R Development Core Team 2018). We used the emmeans function of the emmeans package (Lenth et al. 2018) for post-hoc contrasts of factors from generalised and mixed-effects linear models. R code is publicly archived at Zenodo (Lortie 2018).

Results

Annual plant species were generally more abundant near native foundation shrubs than away from shrubs. Across all species and years, annual plants were 1.35 ($\pm$ 0.68 SE) times more abundant under shrubs than in the open (df = 2381, *t*-value = 12.97, $P < 0.01$). Accordingly, net RII summarised across all species and years was greater than zero (RII = 0.22 $\pm$ 0.05 SE, df = 30.00, *t*-value = 4.98, $P << 0.01$) (Table 1). In addition, RII values summarised across all annual species were greater than zero for each year of the study except 2017 and were never less than zero (Table 1).

In each year of the study, native and exotic annual species positively associated with *E. californica* to become beneficiary species (Fig. 1). Many shrub-annual plant associations were neutral, but none were negative (Fig. 1, Suppl. material 1: Table A3). Interestingly, the only annual species that formed a positive association with *E. californica* across all study years was the exotic invader *B. rubens* (RII = 0.55 $\pm$ 0.16 SE, df = 4.09, *t*-value = 2.72, $P = 0.05$) (Suppl. material 1: Table A3). Shrub size did not affect association patterns at the species level (Suppl. material 1: Table A4).

Interestingly, native and exotic annuals associated differentially with native foundation shrubs at the provenance level. At the provenance level, net RII summarised

Table 1. Mean effects (RII ± SE) of shrubs on annual species at the community level. RII values are summarised across all annual species for each year of the study (2015–2018) and for all study years combined (Net). $P \leq 0.05$ indicates that RII values differ significantly from zero, according to independent *t*-tests.

Year	RII	df	*t*-value	*P*-value
2015	0.18 (0.07)	11.00	2.86	0.01
2016	0.10 (0.05)	8.00	2.21	0.05
2017	0.39 (0.31)	3.00	2.06	0.13
2018	0.38 (0.14)	5.00	3.62	0.01
Net	0.22 (0.05)	30.0	4.98	<<0.01

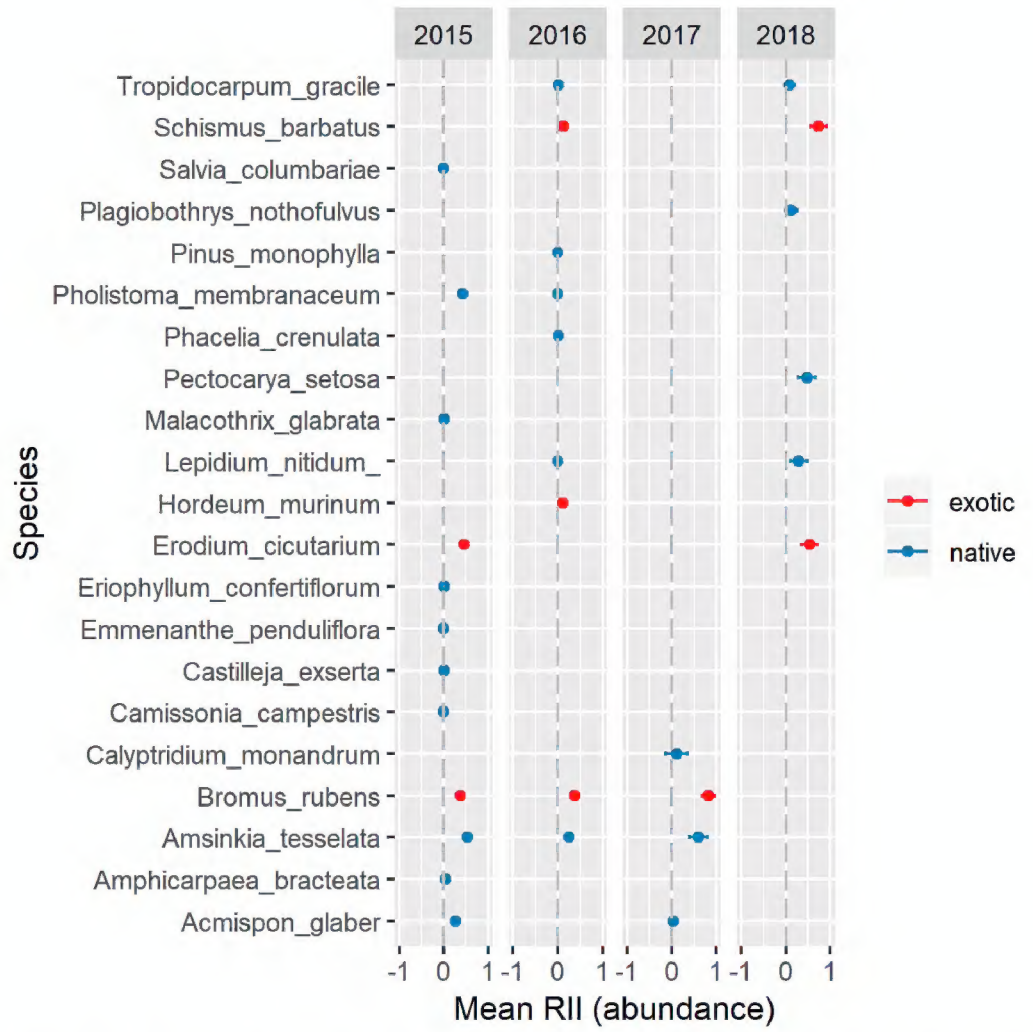

Figure 1. Year-by-year effects (RII ± 95% CI) of native foundation shrubs on the abundance of annual species. Net effects across all years are summarised in Suppl. material 1: Table A3.

Table 2. Mean effects (RII ± SE) of shrubs on annual species at the provenance level. RII values are summarised across native (RII_{native}) and exotic (RII_{exotic}) annual species for each year of the study (2015–2018) and for all study years combined (Net). $P \leq 0.05$ indicates that RII values differ at the provenance level, according to independent generalized linear models (2015–2018) and a linear mixed-effects model (Net).

Year	RII_{native}	RII_{exotic}	df	Z-ratio	*P*-value
2015	0.13 (0.06)	0.41 (0.14)	11.00	1.90	0.05
2016	0.05 (0.05)	0.21 (0.07)	8.00	1.91	0.05
2017	0.25 (0.18)	0.82 (0.30)	3.00	1.61	0.10
2018	0.24 (0.09)	0.64 (0.12)	5.00	2.66	<0.01
Net	0.16 (0.13)	0.44 (0.15)	21.01	*9.28	<0.01

*F-value; see Suppl. material 1: Table A5 for complete statistics

across all years was 2.75 ± 0.14 SE times greater for exotic annuals than for native annuals (df = 21.01, *Z*-ratio = 3.05, $P < 0.01$), and this general trend (i.e., greater RII values for exotic annuals than native annuals at the provenance level) was apparent in each year of the study except 2017 (Table 2). At the provenance level, RII values for native annuals were never greater than RII values for exotic annuals (Table 2). Shrub size did not affect association patterns at the provenance level (Suppl. material 1: Table A5).

Regardless of year and microsite, exotic annual species were always more abundant than native annual species. Summarised across all years, the net abundance of exotic annuals was 4.97 ± 0.78 SE and 3.05 ± 0.78 SE times greater than the net abundance of native annuals in shrub and open microsites, respectively (df ≥ 1863.40, *t*-value ≥ |28.89|, $P < 0.01$) (Suppl. material 1: Table A6). This trend (i.e., greater net abundance of exotic annuals than native annuals) was apparent in shrub and open microsites for each year of the study (Suppl. material 1: Table A6).

At the provenance level, the relationship between the abundance of native and exotic annuals varied considerably by year (Fig. 2). In 2015 and in both shrub and open microsites, native and exotic abundance were negatively related (line slope ≤ -0.25 ± 0.03 SE, df ≥ 838, *t*-value ≥ |8.83|, $P < 0.01$) (Suppl. material 1: Table A7). In 2016–2017, we detected no relationships between native and exotic abundance (df ≥ 28.00, *t*-value ≤ |1.01|, $P \geq 0.31$) (Suppl. material 1: Table A7). In 2018, native and exotic abundance were unrelated in shrub microsites (line slope = 0.04 ± 0.02 SE, df = 22.00, *t*-value = 1.62, $P = 0.12$) but positively related in open microsites (line slope = 0.35 ± 0.04 SE, df = 22.00, *t*-value = 7.88, $P < 0.01$) (Suppl. material 1: Table A7).

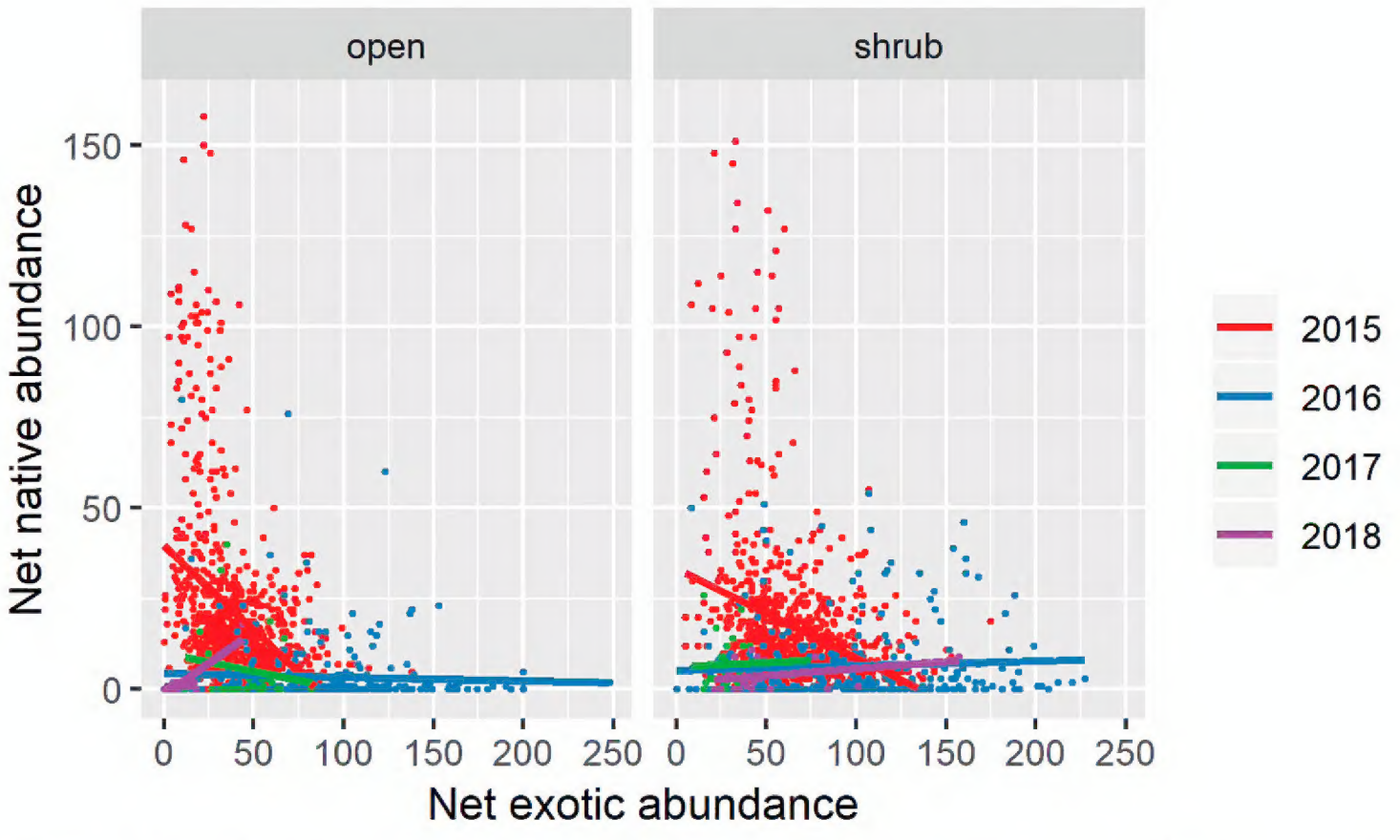

Figure 2. Net abundance of native annuals plotted against net abundance of exotic annuals for each year of the study (2015–2018). Statistics are shown in Suppl. material 1: Table A7.

Discussion

Facilitation is an important process in the assembly of plant communities in drylands and other extreme environments globally (Callaway 2007), but few studies have contrasted the effects of native foundation species on native vs. exotic beneficiary species (but see Reisner et al. 2015; Ramírez et al. 2015; Hupp et al. 2017; Llambi et al. 2018). Understanding how ecological processes affect native and exotic taxa has important implications for the conservation of ecosystems affected by biological invasions (Simberloff et al. 2013, Pearson et al. 2018). In an arid grassland, we found that native and exotic annual species consistently formed positive associations with the native shrub *E. californica*. However, the strength of these associations depended upon the provenance of beneficiary species – at the provenance level, exotic annuals consistently associated more strongly with *E. californica* shrubs than native annuals, and in terms of relative abundance, exotic species always dominated annual plant communities. Thus, the force of facilitation had a dark side at Carrizo Plain.

Our study coincides with a broad literature suggesting that ecological processes can have markedly different effects on native and exotic taxa in the same communities (reviewed by Levine et al. 2003; Mitchell et al. 2006; Catford et al. 2009; Pearson et al. 2018). Most studies have focused on the effects of negative interactions like competition (Seabloom et al. 2003; Vila and Weiner 2004; Callaway et al. 2011) and predation (Maron et al. 2012; Lucero 2018; Lucero and Callaway 2018), but our study is unique in contrasting the effects of positive interactions on native and exotic taxa at the provenance level. The extent that community-level processes have divergent effects on native and exotic neighbours has been hotly debated (Davis et al. 2011; Simberloff 2011) but is an important consideration for explaining, predicting, and managing biological invasions (Pearson et al. 2018).

Our study underscores the potential for facilitation by native foundation species to exacerbate biological invasions. Native foundation species can increase the ecophysiological performance (Cavieres et al. 2008), abundance (Lenz and Facelli 2003; Reisner et al. 2015; Hupp et al. 2017), population growth (Griffith 2010), and spatial distribution (Altieri et al. 2010) of exotic invaders. In addition, facilitation by native foundation species may help explain the initial colonisation of some exotic species in non-native communities (Stohlgren et al. 2006; Fridley et al. 2007). In this context, the initial colonisation of exotic species like *B. rubens*, *Schismus barbatus*, and *Erodium cicutarium* at Carrizo Plain may have been facilitated by native foundation shrubs. However, this interpretation should be viewed with some caution because exotic annuals in this system can clearly colonise open microsites without the aid of shrubs (Suppl. material 1: Table A6). Because exotic annuals were relatively more abundant than native annuals in both shrub and open microsites (Suppl. material 1: Table A6), we argue that shrub facilitation probably reinforced but did not entirely drive the dominance (in terms of relative abundance) of exotic annuals in this system. Our study emphasises the importance of interpreting the effects of ecological processes within the context of net outcomes at the community level (Brooker et al. 2005; Soliveres et al. 2015).

There was considerable inter-annual variation in the effects of *E. californica* on annual species. The strength of positive interactions is known to increase with environmental severity (Bertness and Callaway 1994; Maestre et al. 2009; He et al. 2013; Gao et al. 2018), and environmental severity (i.e., drought and heat stress) can fluctuate widely from year to year in deserts (Venable 2007). In this context, native shrubs facilitated the abundance of the greatest number of species in 2015 (Fig. 1), the study's driest year (Suppl. material 1: Table A2). Drought intensity is predicted to increase in deserts across southwestern North America in the 21st century (Cook et al. 2015). If so, the number of species that associate with shrubs and the strength of these associations may also increase (He et al. 2013; Gao et al. 2018), along with any negative net outcomes of facilitation.

We observed no effects of shrub size on association patterns at either the species or provenance levels (Suppl. material 1: Tables A4, 5). This accords with a recent study by Lortie et al. (2018a) showing that the positive effects of *E. californica* on annual species are independent of canopy size. Our study extends these results by considering the provenance of annuals. In other severe environments, shrub size has strongly influenced the direction and magnitude of association patterns (Tewksbury and Lloyd 2001; Miriti 2006; Brathen and Lortie 2015) and may be an important consideration for other foundation species at Carrizo Plain.

Our study hints that facilitation by *E. californica* shrubs can alter the outcome of interspecific interactions among native and exotic neighbours. In 2018, the abundance of native and exotic annuals was positively related in open microsites (where *E. californica* was absent) but unrelated in shrub microsites (where *E. californica* was present). These relationships suggest facilitation between native and exotic annuals in open but not shrub microsites. Thus, it is possible that *E. californica* attenuated positive interactions between native and exotic annuals in that year. Facilitation of native species by exotic neighbours – including invasive species – is not necessarily unusual in deserts. For instance, in the Great Basin Desert, Lucero et al. (2015) found evidence that the native perennial grass *Elymus elymoides* was more abundant and produced a significantly greater seed rain in areas invaded by exotic *Bromus tectorum* than in adjacent non-invaded areas. Thus, invasive species do not always impose negative effects on native neighbours. Importantly, a positive relationship between native and exotic abundance does not necessarily indicate facilitation; native and exotic plants could both respond favourably to particularly good microsites.

Our study highlights the potential for beneficiary species to experience facilitation from foundation species and interspecific competition from other beneficiary species simultaneously. In 2015, competition and facilitation appeared to operate in tandem to influence biodiversity patterns under shrubs (Fig. 2, Tables 1, 2). This coincides with a number of recent studies (Maestre et al. 2004, Poulos et al. 2014; Sheley and James 2014; Wright et al. 2014; Reisner et al. 2015; Llambi et al. 2018). The relative importance (*sensu* Brooker et al. 2005) of these biotic interactions likely depends upon abiotic conditions and the ontological development of interacting species (Callaway et al. 1996; Fagundes et al. 2018; Gao et al. 2018; Pierce et al. 2018).

We hypothesised that any competitive effects of exotic annuals on native annuals in 2015 may have been driven by *B. rubens*, as this exotic species was facilitated more strongly and consistently than any other (Fig. 1, Suppl. material 1: Table A3). To test this, we regressed the abundance of native annuals (all species combined) against the abundance of *B. rubens* for each year of the study. We found no negative relationship between the net abundance of native annual species and *B. rubens* in 2015 or any other year (Suppl. material 1: Fig. A1), suggesting that any competitive effects of exotics on natives were not driven by *B. rubens* alone. However, it is important to note that *B. rubens* has strongly reduced the abundance of native competitors in arid environments similar to our study system (Brooks 2000; Salo 2005). The source of such context-dependence is unclear, but the presence of competitive interactions between native and invasive species at fine spatial scales is consistent with an extensive literature (reviewed by Levine et al. 2003; Vila and Weiner 2004; Mitchell et al. 2006; Liao et al. 2008; Vila et al. 2011).

Our data do not speak to the mechanisms by which facilitation occurred. Non-mutually exclusive mechanisms of facilitation include seed trapping, amelioration of abiotic stress, modification of soil biogeochemical processes, increasing pollinator visitation, and/or providing herbivore protection (reviewed by Filazzola and Lortie 2014). Importantly, we do not know whether native and exotic species were facilitated via the same mechanisms. If native and exotic species generally capitalise on different mechanisms of facilitation, conservationists could potentially manage biological invasions by disrupting the mechanistic pathways specific to exotics.

Our findings have practical implications. Because *E. californica* canopies were hotspots for the abundance of native and exotic annual species, conservationists may consider targeting their efforts to control invasive species under shrub canopies. For example, herbicide applications to reduce the density of invasive species and subsequent reseeding efforts to increase the density of native species (Huddleston and Young 2005; Rowe 2010; Clements et al. 2017) might yield the greatest dividends if focused under shrub canopies. In addition, reducing the density of *B. rubens* and *S. barbatus* under shrub canopies could help decrease wildfire risk by reducing fine fuel loads (Brooks 1999; Brooks et al. 2004). Positive feedbacks between wildfire and the abundance of exotic invaders are well documented (reviewed by D'Antonio and Vitousek 1992; Brooks et al. 2004), and wildfire-invasion feedbacks may cause rapid state changes in dryland vegetation (Balch et al. 2013; Horn and St. Clair 2017).

Furthermore, our study suggests caution in using facilitation by native shrubs as a tool for restoring native biodiversity to degraded environments. Drylands in California and globally are being retired from intensive agricultural use due to drought, poor soils, and changing climate (Webb et al. 2017), presenting critical opportunities for restoring native biodiversity (Kelsey et al. 2018; Lortie et al. 2018c). In this context, facilitation by native shrubs has attracted considerable interest as a restoration tool (Padilla and Pugnaire 2006; Funk et al. 2008; Gomez-Aparicio 2009; Lortie et al. 2018c). However, strong facilitation of exotic and invasive species by *E. californica* could undermine restoration efforts in our study area. For instance, the San Joaquin kit fox (*Vulpes macrotis* ssp. *mutica*) is an endangered species endemic to the San Joaquin Desert (Williams

et al. 1998) that has been identified as a potential target for restoration (Lortie et al. 2018c). Importantly, kit foxes avoid areas with high densities of exotic grass species like *B. rubens*, *S. barbatus*, and *Hordeum murinum* (Smith et al. 2005). Accordingly, facilitation of these exotic grass species by *E. californica* (Fig. 1) could be counterproductive to the restoration of kit foxes and many other wildlife species that avoid areas with high densities of exotic grasses (Ostoja and Schupp 2009; Freeman et al. 2014; Filazzola et al. 2017). Our study highlights the need for ecological restoration based on facilitation to be tailored to the species and environments in question (Noumi et al. 2015).

Conclusions

Our study reaffirms facilitation as an important force in the organisation of plant communities and confirms that both native and exotic beneficiary species can positively associate with native foundation shrubs. However, we found that the magnitude of facilitation depended upon the biogeographic origins of beneficiary species – at the provenance level, exotic species were facilitated in abundance much stronger than native species. Importantly and regardless of inter-annual variation in climate, the net outcome of biotic interactions that included facilitation was an annual plant community dominated (in terms of relative abundance) by exotic species. Our study stresses that the effects of ecological processes like facilitation must not be decoupled from net outcomes relevant to conservation and restoration. In systems like ours where facilitation increases the abundance of invasive species, managing positive interactions may be a useful conservation strategy.

Acknowledgements

This research was funded by a TNC grant, BLM funds, and an NSERC DG to CJL. JEL was supported by a York Science Fellowship. Ray Callaway provided excellent editorial input.

References

Allington GRH, Koons DN, Morgan Ernest SK, Schutzenhofer MR, Valone TJ (2013) Niche opportunities and invasion dynamics in a desert annual community. Ecology Letters 16: 158–166. https://doi.org/10.1111/ele.12023

Altieri AH, van Wesenbeeck BK, Bertness MD, Silliman BR (2010) Facilitation cascade drives positive relationship between native biodiversity and invasion success. Ecology 91: 1269–1275. https://doi.org/10.1890/09-1301.1

Armas C, Ordinales R, Pugnaire FI (2004) Measuring plant interactions: a new comparative index. Ecology 85: 2682–2686. https://doi.org/10.1890/03-0650

Badano EI, Bustamante RO, Villarroel E, Marquet PA, Cavieres LA (2015) Facilitation by nurse plants regulates community invasibility in harsh environments. Journal of Vegetation Science 26: 756–767. https://doi.org/10.1111/jvs.12274

Balch JK, Bradley BA, D'Antonio CM, Gomez-Dans J (2013) Introduced annual grass increases regional fire activity across the arid western USA (1980–2009). Global Change Biology 19: 173–183. https://doi.org/10.1111/gcb.12046

Baxter CV, Fausch KD, Murakami M, Chapman PL (2004) Fish invasion restructures stream and forest food webs by interrupting reciprocal prey subsidies. Ecology 85: 2656–2663. https://doi.org/10.1890/04-138

Bellard C, Cassey P, Blackburn TM (2016) Alien species as a driver of recent extinctions. Biology Letters 12. https://doi.org/10.1098/rsbl.2015.0623

Bertness MD, Callaway RM (1994) Positive interactions in communities. Trends in Ecology and Evolution 9: 191–193. https://doi.org/10.1016/0169-5347(94)90088-4

Blackburn TM, Pysek P, Bacher S, Carlton JT, Duncan RP, Jarosik V, Wilson JRU, Richardson DM (2011) A proposed unified framework for biological invasions. Trends in Ecology and Evolution 26: 333–339. https://doi.org/10.1016/j.tree.2011.03.023

Brathen KA, Lortie CJ (2015) A portfolio effect of shrub canopy height on species richness in both stressful and competitive environments. Functional Ecology 30:60–69. https://doi.org/10.1111/1365-2435.12458

Brooker RW, Maestre FT, Callaway RM, Lortie CL, Cavieres LA, Kunstler G, Linacourt P, Tielborger K, Travis JM, Anthelme F, Armas C, Coll L, Corcket E, Delzon S, Forey E, Kikvidze Z, Olofsson J, Pugnaire F, Quiroz C, Saccone P, Schiffers K, Seifan M, Touzard B, Micharet R (2008) Facilitation in plant communities: the past, the present, and the future. Journal of Ecology 96: 18–34.

Brooker R, Kikvidze Z, Pugnaire FI, Callaway RM, Choler P, Lortie CJ, Michalet R (2005) The importance of importance. Oikos 109: 63–70. https://doi.org/10.1111/j.0030-1299.2005.13557.x

Brooks ML (1999) Alien annual grasses and fire in the Mojave Desert. Madroño 46: 13–19.

Brooks ML (2000) Competition between alien annual grasses and native annual plants in the Mojave Desert. The American Midland Naturalist 144: 92–108. https://doi.org/10.1674/0003-0031(2000)144[0092:CBAAGA]2.0.CO;2

Brooks ML, D'Antonio CM, Richardson DM, Grace JB, Keeley JE, DiTomaso JM, Hobbs RJ, Pellant M, Pyke D (2004) Effects of invasive alien plants on fire regimes. BioScience 54: 677–688. https://doi.org/10.1641/0006-3568(2004)054[0677:EOIAPO]2.0.CO;2

Buck-Diaz J, Evens J (2011) Carrizo Plain National Monument vegetation classification and mapping project.

Butterfield BJ, Cavieres LA, Callaway RM, Cook J, Kikvidze Z, Lortie CJ, Michalet R, Pugnaire FI, Schob C, Xiao S, Zaitchek B, Anthelme F, Bjork RG, Dickinson K, Gavilan R, Kanka R, Maalouf JP, Noroozi J, Parajuli R, Phoenix GK, Reid A, Ridenour W, Rixen C, Wipf S, Zhao L, Brooker RW (2013) Alpine cushion plants inhibit the loss of phylogenetic diversity in severe environments. Ecology Letters 16: 478–486. https://doi.org/10.1111/ele.12070

Calflora (2018) Information on California plants for education, research and conservation, with data contributed by public and private institutions and individuals, including the

Consortium of California Herbaria. Berkeley, California. https://www.calflora.org/ [Accessed: September 20, 2018]

Callaway RM (1995) Positive interactions among plants. The Botanical Review 61: 306–349. https://doi.org/10.1007/BF02912621

Callaway RM, DeLucia EH, Moore D, Nowak R, Schlesinger WH (1996) Competition and facilitation: contrasting effects of *Artemisia tridentata* on desert vs. montane pines. Ecology 77: 2130–2141. https://doi.org/10.2307/2265707

Callaway RM (2007) Positive interactions and interdependence in plant communities. Springer, Dordrecht, The Netherlands.

Callaway RM, Waller LP, Diaconu A, Pal R, Collins AR, Mueller-Schaerer H, Maron JL (2011) Escape from competition: neighbors reduce *Centaurea stoebe* performance at home but not away. Ecology 92: 2208–2213. https://doi.org/10.1890/11-0518.1

Catford JA, Jansson R, Nilsson C (2009) Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. Diversity and Distributions 15: 22–40. https://doi.org/10.1111/j.1472-4642.2008.00521.x

Cavieres LA, Quiroz CL, Molina-Montenegro MA (2008) Facilitation of the non-native *Taraxacum officinale* by native nurse cushion species in the high Andes of central Chile: are there differences between nurses? Functional Ecology 22: 148–156.

Cook BI, Ault TR, Smerdon JE (2015) Unprecedented 21st century drought risk in the American Southwest and Central Plains. Science Advances 1: e1400082. https://doi.org/10.1126/sciadv.1400082

Clements CD, Harmon DN, Blank RR, Weltz M (2017) Improving seeding success on cheatgrass-infested rangelands in northern Nevada. Rangelands 39: 174–181. https://doi.org/10.1016/j.rala.2017.10.003

Cutlar HC (1939) Monograph of the North American species of the genus *Ephedra*. Annals of the Missouri Botanical Garden 26: 373–428. https://doi.org/10.2307/2394299

D'Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annual Review of Ecology and Systematics 23: 63–87. https://doi.org/10.1146/annurev.es.23.110192.000431

Davis MH et al. (2011) Don't judge species on their origins. Nature 474: 153–154. https://doi.org/10.1038/474153a

Fagundes M, Weisser W, Ganade G (2018) The role of nurse successional stages on species-specific facilitation in drylands: nurse traits and facilitation skills. Ecology and Evolution 8: 5173–5184. https://doi.org/10.1002/ece3.3962

Filazzola A, Lortie CJ (2014) A systematic review and conceptual framework for the mechanistic pathways of nurse plants. Global Ecology and Biogeography 23:1335–1345. https://doi.org/10.1111/geb.12202

Filazzola A, Westphal M, Powers M, Liczner AR, (Smith) Woollett DA, Johnson B, Lortie CJ (2017) Non-trophic interactions in deserts: facilitation, interference, and an endangered lizard species. Basic and Applied Ecology 20: 51–61. https://doi.org/10.1016/j.baae.2017.01.002

Filazzola A, Sotomayor DA, Lortie CJ (2018) Modelling the niche space of desert annuals to include positive interactions. Oikos 127: 264–273. https://doi.org/10.1111/oik.04688

Foronda A, Pueyo Y, Arroyo AI, Saiz H, de la Luz Giner M, Alados CL (2019) The role of nurse shrubs on the spatial patterning of plant establishment in semi-arid gypsum plant communities. Journal of Arid Environments 160: 82–90. https://doi.org/10.1016/j.jaridenv.2018.09.003

Freeman ED, Sharp TR, Larsen RT, Knight RN, Slater SJ, McMillan BR (2014) Negative effects of an exotic grass invasion on small-mammal communities. PLoS ONE 9: e108843. https://doi.org/10.1371/journal.pone.0108843

Fridley JD, Stachowicz JJ, Naeem S, Sax DF, Seabloom EW, Smith MD, Stohlgren TJ, Tilman D, Von Holle B (2007) The invasion paradox: reconciling pattern and process in species invasions. Ecology 88: 3–7. https://doi.org/10.1890/0012-9658(2007)88[3:TIPRPA]2.0.CO;2

Funk JL, Cleland EE, Suding KN, Zavaleta ES (2008) Restoration through reassembly: plant traits and invasion resistance. Trends in Ecology and Evolution 23: 695–703. https://doi.org/10.1016/j.tree.2008.07.013

Gao X, Liu Z, Zhao X, Ling Q, Huo G, Wu P (2018) Extreme natural drought enhances interspecific facilitation in semiarid agroforestry systems. Agriculture, Ecosystems & Environment 265: 444–453. https://doi.org/10.1016/j.agee.2018.07.001

Germano DJ, Rathburn GB, Saslaw LR, Cypher BL, Cypher EA, Vredenburgh LM (2011) The San Joaquin Desert of California: ecologically misunderstood and overlooked. Natural Areas Journal 31: 138–147. https://doi.org/10.3375/043.031.0206

Gomez-Aparicio L (2009) The role of plant interactions in the restoration of degraded ecosystems: a meta-analysis across life-forms and ecosystems. Journal of Ecology 97: 1202–1214. https://doi.org/10.1111/j.1365-2745.2009.01573.x

Griffith AB (2010) Positive effects of native shrubs on *Bromus tectorum* demography. Ecology 91: 141–154. https://doi.org/10.1890/08-1446.1

He Q, Bertness MD, Altieri AH (2013) Global shifts towards positive species interactions with increasing environmental stress. Ecology Letters 16: 695–706. https://doi.org/10.1111/ele.12080

Horn KJ, St. Clair SB (2017) Wildfire and exotic grass invasion alter plant productivity in response to climate variability in the Mojave Desert. Landscape Ecology 32: 635–646. https://doi.org/10.1007/s10980-016-0466-7

Huddleston RT, Young TP (2005) Weed control and soil amendment effects on restoration plantings in an Oregon grassland. Western North American Naturalist 65: 507–515.

Hupp N, Llambi LD, Ramírez L, Callaway RM (2017) Alpine cushion plants have species-specific effects on microhabitat and community structure in the tropical Andes. Journal of Vegetation Science 28: 928–938. https://doi.org/10.1111/jvs.12553

Jeschke JM, Aparicio LG, Haider S, Heger T, Lortie CJ, Pysek P, Strayer D (2012) Support for major hypotheses in invasion biology is uneven and declining. NeoBiota 14: 1–20. https://doi.org/10.3897/neobiota.14.3435

Kelsey R, Hart A, Butterfield HS, Vink D (2018) Groundwater sustainability in the San Joaquin Valley: multiple benefits if agricultural lands are retired and restored strategically. California Agriculture 72: 151–154. https://doi.org/10.3733/ca.2018a0029

Kuznetsova A, Brockhoff PB, Christensen RHB (2017) lmerTest Package: Tests in Linear Mixed Effects Models. Journal of Statistical Software 82: 1–26. https://doi.org/10.18637/jss.v082.i13

Lenth R, Singmann H, Love J, Buerkner P, Herve M (2018) Package 'emmeans'. https://github.com/rvlenth/emmeans

Lenz TI, Facelli JM (2003) Shade facilitates an invasive stem succulent in a chenopod shrubland in South Australia. Austral Ecology 28: 480–490. https://doi.org/10.1046/j.1442-9993.2003.01304.x

Levine JM, Vila M, D'Antonio CM, Dukes JD, Grigulis K, Lavorel S (2003) Mechanisms underlying the impacts of exotic plant invasions. Proceedings of the Royal Society B 270: 775–781. https://doi.org/10.1098/rspb.2003.2327

Liao C, Peng R, Lup Y, Zhou X, Wu X, Fang C, Chen J, Li B (2008) Altered ecosystem carbon and nitrogen cycles by plant invasion: a meta-analysis. New Phytologist 177: 706–714. https://doi.org/10.1111/j.1469-8137.2007.02290.x

Llambi LD, Hupp N, Saez A, Callaway RM (2018) Reciprocal interactions between a facilitator, natives, and exotics in tropical alpine plant communities. Perspectives in Plant Ecology, Evolution, and Systematics. 30: 82–88. https://doi.org/10.1016/j.ppees.2017.05.002

Lortie CJ (2018) Carrizo long-term ecological data analyses. Zenodo.

Lortie CJ, Gruber E, Filazzola A, Noble T, Westphal M (2018a) The Groot effect: plant facilitation and desert shrub regrowth following extensive damage. Ecology and Evolution 8: 706–715. https://doi.org/10.1002/ece3.3671

Lortie CJ, Noble T, Haas S, Butterfield S, Lucero J, Westphal M (2018b) Long-term ecological vegetation data for Carrizo National Monument, California. Knowledge Network for Biocomplexity.

Lortie CJ, Filazzola A, Kelsey R, Hart AK, Butterfield S (2018c) Better late than never: a synthesis of strategic land retirement and restoration in California. Ecosphere 9: e02367. https://doi.org/10.1002/ecs2.2367

Lucero JE, Allen PS, McMillan BR (2015) Increased primary production from an exotic invader does not subsidize native rodents. PLoS ONE 10(8): e0131564. https://doi.org/10.1371/journal.pone.0131564

Lucero JE (2018) Do seeds from invasive bromes experience less granivory than seeds from native congeners in the Great Basin Desert? Plant Ecology 219: 1053–1061. https://doi.org/10.1007/s11258-018-0858-7

Lucero JE, Callaway RM (2018) Native granivores reduce the establishment of native grasses but not invasive *Bromus tectorum*. Biological Invasions 20: 3491–3497. https://doi.org/10.1007/s10530-018-1789-x

Maestre FT, Callaway RM, Valladares F, Lortie CJ (2009) Refining the stress-gradient hypothesis for competition and facilitation in plant communities. Journal of Ecology 2009: 199–205. https://doi.org/10.1111/j.1365-2745.2008.01476.x

Maestre FT, Cortina J, Bautista S (2004) Mechanisms underlying the interaction between *Pinus halipensis* and the native late-successional shrub *Pistacia lentiscus* in a semi-arid plantation. Ecography 27: 776–786. https://doi.org/10.1111/j.0906-7590.2004.03990.x

Maron JL, Vila M (2001) When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypotheses. Oikos 95: 361–373. https://doi.org/10.1034/j.1600-0706.2001.950301.x

Maron JL, Pearson DE, Potter T, Ortega YK (2012) Seed size and provenance mediate the joint effects of disturbance and seed predation on community assembly. Journal of Ecology 100: 1492–1500. https://doi.org/10.1111/j.1365-2745.2012.02027.x

McIntire EJB, Fajardo A (2014) Facilitation as a ubiquitous driver of biodiversity. New Phytologist 201: 403–416. https://doi.org/10.1111/nph.12478

Michalet R (2006) Is facilitation in arid environments the result of direct or complex interactions? New Phytologist 169: 3–6. https://doi.org/10.1111/j.1468-8137.2006.01617.x

Michalet R, Pugnaire FI (2016) Facilitation in communities: underlying mechanisms, community and ecosystem implications. Functional Ecology 30: 3–9. https://doi.org/10.1111/1365-2435.12602

Miriti LM (2006) Ontogenetic shift from facilitation to competition in a desert shrub. Journal of Ecology 94: 973–979. https://doi.org/10.1111/j.1365-2745.2006.01138.x

Mitchell CE, Agrawal AA, Bever JD, Gilbert GS, Hufbauer RA, Klironomos JN, Maron JL, Morris WF, Parker IM, Power AG, Seabloom EW, Torchin ME, Vazquez DP (2006) Biotic interactions and plant invasions. Ecology letters 9: 726–740. https://doi.org/10.1111/j.1461-0248.2006.00908.x

Noble TJ, Lortie CJ, Westphal M, Butterfield HS (2016) A picture is worth a thousand data points: an imagery dataset of paired shrub-open microsites within Carrizo Plain National Monument. GigaScience 5. https://doi.org/10.1186/s13742-016-0145-2

Noumi Z, Chaieb M, Michalet R, Touzard B (2015) Limitations to the use of facilitation as a restoration tool in arid grazed savanna: a case study. Applied Vegetation Science 18: 391–401. https://doi.org/10.1111/avsc.12158

Ostoja SM, Schupp EW (2009) Conversion of sagebrush shrublands to exotic annual grasslands negatively impacts small mammal communities. Diversity and Distributions 15: 863–870. https://doi.org/10.1111/j.1472-4642.2009.00593.x

Padilla FM, Pugnaire FI (2006) The role of nurse plants in the restoration of degraded environments. Frontiers in Ecology and the Environment 4: 196–202. https://doi.org/10.1890/1540-9295(2006)004[0196:TRONPI]2.0.CO;2

Pearson DE, Callaway RM (2008) Weed-biocontrol insects reduce native-plant recruitment through second-order apparent competition. Ecological Applications 18: 1489–1500. https://doi.org/10.1890/07-1789.1

Pearson DE, Ortega YK, Ozkan E, Hierro JL (2016) Quantifying "apparent" impact and distinguishing impact from invasiveness in multispecies plant invasions. Ecological Applications 26: 162–173. https://doi.org/10.1890/14-2345

Pearson DE, Ortega YK, Ozkan E, Hierro JL (2018) Community assembly theory as a framework for biological invasions. Trends in Ecology & Evolution 33: 313–325. https://doi.org/10.1016/j.tree.2018.03.002

Pescador DS, Chacon-Labella J, de la Cruz M, Escudero A (2014) Maintaining distances with the engineer: patterns of coexistence in plant communities beyond the patch-bare dichotomy. New Phytologist 204: 140–148. https://doi.org/10.1111/nph.12899

Pierce NA, Archer SR, Bestelmeyer BT, James DK (2018) Grass-shrub competition in arid lands: an overlooked driver in grassland-shrubland state transition? Ecosystems. https://doi.org/10.1007/s10021-018-0290-9

Poulos JM, Rayburn AP, Schupp EW (2014) Simultaneous, independent, and additive effects of shrub facilitation and understory competition on the survival of a native forb (*Penstemon palmeri*). Plant Ecology: 417–426. https://doi.org/10.1007/s11258-014-0312-4

Pucheta E, Garcia-Munro VJ, Rolhauser AG, Quevedo-Robledo L (2011) Invasive potential of the winter grass *Schismus barbatus* during the winter season of a predominantly summer-rainfall desert in Central-Northern Monte. Journal of Arid Environments 75: 390–393. https://doi.org/10.1016/j.jaridenv.2010.11.010

R Development Core Team (2018) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ramírez L, Rada F, Llambí LD (2015) Linking patterns and processes through ecosystem engineering: effects of shrubs on microhabitat and water status of associated plants in the high tropical Andes. Plant Ecology 216: 213–225. https://doi.org/10.1007/s11258-014-0429-5

Reisner MD, Doescher PS, Pyke DA (2015) Stress-gradient hypothesis explains susceptibility to *Bromus tectorum* invasion and community stability in North America's semi-arid *Artemisia tridentata wyomingensis* ecosystems. Journal of Vegetation Science 26: 1212–1224. https://doi.org/10.1111/jvs.12327

Rowe HI (2010) Tricks of the trade: techniques and opinions from 38 experts in tallgrass prairie restoration. Restoration Ecology 18: 253–262. https://doi.org/10.1111/j.1526-100X.2010.00663.x

Salo LF (2005) Red brome (*Bromus rubens* subsp. *madritensis*) in North America: possible modes for early introductions, subsequent spread. Biological Invasions 7: 165–180. https://doi.org/10.1007/s10530-004-8979-4

Schutzenhofer MR, Valone TJ (2006) Positive and negative effects of *Erodium cicutarium* on an arid ecosystem. Biological Conservation 132: 376–381. https://doi.org/10.1016/j.biocon.2006.04.031

Seabloom EW, Harpole WS, Reichman OJ, Tilman D (2003) Invasion, competitive dominance, and resource use by exotic and native California grassland species. Proceedings of the Royal Academy of Science 100: 13384–13389. https://doi.org/10.1073/pnas.1835728100

Sheley RL, James JJ (2014) Simultaneous intraspecific facilitation and interspecific competition between native and annual grasses. Journal of Arid Environments 104: 80–87. https://doi.org/10.1016/j.jaridenv.2014.01.019

Simberloff D (2006) Invasional meltdown 6 years later: important phenomenon, unfortunate metaphor, or both? Ecology Letters 9: 912–919. https://doi.org/10.1111/j.1461-0248.2006.00939.x

Simberloff D (2011) Non-natives: 141 scientists object. Nature 475: 35–36. https://doi.org/10.1038/475036a

Simberloff D, Martin JL, Genovesi P, Maris V, Wardle WA, Aronson J, Courtchamp F, Galil B, Garcia-Bethou E, Pascal M, Pysek P, Sousa R, Tabacchi E, Vila M (2013) Impacts of biological invasions: what's what and the way forward. Trends in Ecology and Evolution 28: 58–66. https://doi.org/10.1016/j.tree.2012.07.013

Simberloff D, Von Holle B (1999) Positive interactions of nonindigenous species: invasional meltdown? Biological Invasions 1: 21–32. https://doi.org/10.1023/A:1010086329619

Simpson A, Eyler MC (2018) First comprehensive list of non-native species established in three major regions of the United States. U.S. Geological Survey Open-File Report 2018–1156. https://doi.org/10.3133/ofr20181156

Smith DA, Ralls K, Cypher BL, Maldonado JE (2005) Assessment of scat-detection dog surveys to determine kit fox distribution. Wildlife Society Bulletin 33: 897–904. https://doi.org/10.2193/0091-7648(2005)33[897:AOSDST]2.0.CO;2

St. Clair SB, O'Conner R, Gill R, McMillan B (2016) Biotic resistance and disturbance: rodent consumers regulate post-fire plant invasions and increase plant community diversity. Ecology 97: 1700–1711. https://doi.org/10.1002/ecy.1391

Stohlgren TJ, Jarnevich C, Chong GW, Evangelista PH (2006) Scale and plant invasions: a theory of biotic acceptance. Preslia 78: 405–426.

Tewksbury JJ, Lloyd JD (2001) Positive interactions under nurse-plants: spatial scale, stress gradients and foundation species size. Oecologia 127: 425–434. https://doi.org/10.1007/s004420000614

U.S. Department of the Interior Bureu of Land Management (2011) Check list of plants Carrizo Plain, San Luis Obispo County, California. http://www.blm.gov/ca/st/en/fo/bakersfield/ Programs/carrizo/plants.html [retrieved 11-12-2018]

Venable DL (2007) Bet hedging in a guild of desert annuals. Ecology 88: 1086–1090. https://doi.org/10.1890/06-1495

Vila M, Espinar JL, Hejda M, Hulme P, Jarosik V, Maron J, Pergl J, Schaffner U, Sun Y, Pysek P (2011) Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities, and ecosystems. Ecology Letters 14: 702–708. https://doi.org/10.1111/j.1461-0248.2011.01628.x

Vila M, Weiner J (2004) Are invasive plant species better competitors than native plant species? – evidence from pairwise experiments. Oikos 105: 229–238. https://doi.org/10.1111/j.0030-1299.2004.12682.x

Villareal-Barajas T, Martorell C (2009) Species-specific disturbance tolerance, competition and positive interactions along an anthropogenic disturbance gradient. Journal of Vegetation Science 20: 1027–1040. https://doi.org/10.1111/j.1654-1103.2009.01101.x

Vitousek PM, D'Antonio CM, Loope LL, Westbrooks R (2017) Biological invasions as global environmental change.

Webb N, Marshall N, Stringer L, Reed M, Chappell A, Herrick J (2017) Land degradation and climate change: building climate resilience in agriculture. Frontiers in Ecology and the Environment 15: 450–459. https://doi.org/10.1002/fee.1530

Westphal MF, Noble T, Butterfield HS, Lortie CJ (2018) A test of desert shrub facilitation via radiotelemetric monitoring of a diurnal lizard. Ecology and Evolution 8: 12153–12162. https://doi.org/10.1002/ece3.4673

Williams DF, Cypher EA, Kelly PA, Miller KJ, Norvell N, Phillips SF, Johnson CD, Colliver GW (1998) Recovery plan for upland species of the San Joaquin Valley, California. Endangered Species Recovery Program 1: 311–319.

Wright A, Schnitzer SA, Reich PB (2014) Living close to your neighbors: the importance of both competition and facilitation in plant communities. Ecology 95: 2213–2223. https://doi.org/10.1890/13-1855.1

Zarnetske PL, Gouhier TC, Hacker SD, Seabloom EW, Bokil VA (2013) Indirect effects and facilitation among native and non-native species promote invasion success along an environmental stress gradient. Journal of Ecology 101: 905–915. https://doi.org/10.1111/1365-2745.12093

Supplementary material 1

Supplementary materials

Authors: Jacob E. Lucero, Taylor Noble, Stephanie Haas, Michael Westphal, H. Scott Butterfield, Christopher J. Lortie

Data type: multimedia

Explanation note: Supplementary materials for this article are included in Appendix A1, which consists of one supplementary figure (Fig. A1) and seven supplementary tables (Tables A1–A7).

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/neobiota.44.33771.suppl1